

Genetic Diversity of Oceanic Island *Lasaea* (Mollusca: Bivalvia) Lineages Exceeds That of Continental Populations in the Northwestern Atlantic

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Abstract. Direct-developing lineages of the intertidal marine bivalve *Lasaea* have colonized both upstream mainland (southeastern Florida) and downstream oceanic island (Bermuda) locations in the western North Atlantic. Replicate samples from these two regional populations, separated by about 1500 km of open ocean, were sequenced for a 655-nucleotide portion of the mitochondrial (mt) cytochrome oxidase subunit I gene. Twelve haplotypes (2 Floridian and 10 Bermudan) were obtained that differed by a maximum of four substitutions among pairwise comparisons. Phylogenetic analysis yielded a parsimony network within which the mainland lineages clustered in one of the terminal branches; a mirror image of *a priori* expectations based on regional surface-current polarity. It is difficult, however, to envisage a plausible countercurrent dispersal mechanism. This tree topology may stem from divergent demographic processes operating on these two evolutionarily recent regional populations. The starlike phylogenetic pattern of Bermudan lineages is consistent with a history of rapid population growth. The restricted genetic repertoire and relative ecological scarcity of Floridian lineages imply either a recent founder event by unstudied Caribbean source populations or else a history of pronounced bottlenecks in population size. Bermuda's impoverished Caribbean marine biota may allow western North Atlantic *Lasaea* lineages to escape severe competitive interactions impacting other parts of their geographic range.

Introduction

Oceanic islands have never been connected to continental landmasses and represent some of the most isolated environments on earth (Nunn, 1994). They receive their biotas solely through dispersal from geographically distant source populations and from subsequent *in situ* diversification (Paulay, 1994). Stretches of deep ocean surrounding such islands represent dispersal filters for benthic shallow-water marine taxa. The stringency of these filters varies according to physical parameters (*e.g.*, distance from potential source populations, current speed and polarity) and to taxon-specific life-history traits including presence of a prolonged pelagic larval ontogeny (Scheltema, 1992; Jaekle, 1994; Palumbi *et al.*, 1997; Lessios *et al.*, 1998), rafting ability (Jokiel, 1990; Helmuth *et al.*, 1994; Ingólfsson, 1995; Ó Foighil *et al.*, 1999), and propensity for anthropogenic transfer (Carlton, 1989; Carlton and Geller, 1993; Carlton and Hodder, 1995). In general, classical oceanic island biotas exhibit a depauperate and disharmonic composition that may include relict taxa and endemic radiations (Paulay, 1994).

Bermuda is composed of a cluster of small western North Atlantic oceanic islands (32°18'N, 64°46'W) rising from a 65-km² carbonate platform and supported by a submerged volcanic peak (Nunn, 1994; Sterrer, 1998). It is situated within the warm Sargasso Sea section of the North Atlantic Gyre, about 1000 km east of the coast of North Carolina, and the main flow of the Gulf Stream System arcs well to the west and north of its position (Fig. 1). However, the Bermuda Platform is regularly approached by mesoscale anticyclonic eddies originating from the Gulf Stream System (Parker, 1971; Spitzer, 1989). It is generally assumed that Bermuda has remained stable throughout the Quater-

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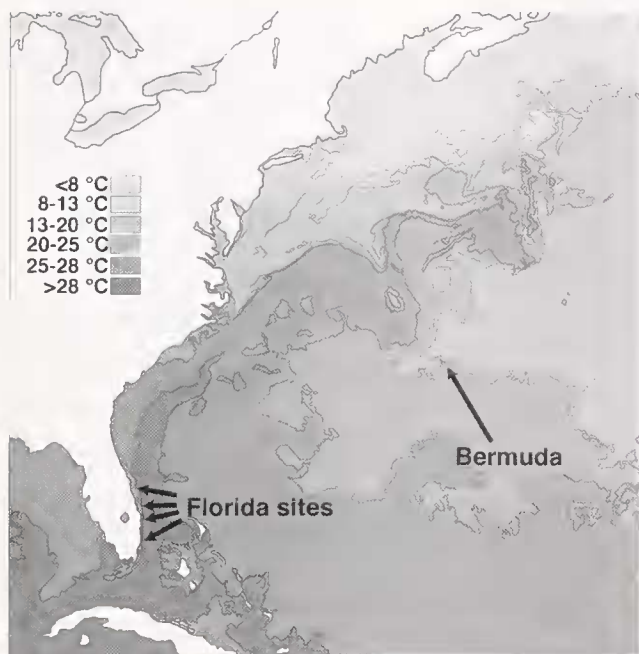


Figure 1. Location of the *Lasaea* sampling sites in the western North Atlantic, plotted onto a satellite image of sea-surface temperatures (modified from Thurman, 1997). The body of warm water flowing through the Florida Straits represents the Florida Current portion of the Gulf Stream System. Past Cape Hatteras, the Gulf Stream proper leaves the continental slope and develops a series of meanders that pinch off persistent mesoscale eddies. Cold eddies migrate southward and approach Bermuda.

nary (Nunn, 1994) and, although late Pleistocene (last 130,000 years) sea-level changes ranged up to 25 m, the island group was not submerged during this period (Harmon *et al.*, 1978, 1981).

The Bermudan shallow-water marine fauna encompasses a low level (2.4%) of endemic species and represents a moderately impoverished oceanic extension of the Caribbean fauna (Sterrer, 1986, 1998). Twenty-eight of a total of 49 common nearshore molluscs found throughout the Caribbean also occur on this oceanic island platform (Warmke and Abbott, 1961), and there is some evidence for a partial turnover of the Bermudan marine malacofauna on ecological timescales (Abbott and Jensen, 1967; Sterrer, 1986). The nearest source populations for Bermudan marine taxa of Caribbean origin are about 1500 km to the southwest, in southern Florida and the Bahamas. Based on net transport of drift bottles, this distance represents a minimum passage of 21–30 days for passive pelagic transport of larvae or rafted propagules (Jackson, 1986). Such a time frame does not pose a serious obstacle for species with long-lived pelagic larvae, but may approach the upper limit for many species with faster developing pelagic larval stages. The few data available on genetic distances of Bermudan marine invertebrates from Caribbean conspecifics are consistent with this view (Mitton *et al.*, 1989; Hateley and Sleeter, 1993). A

number of Bermudan marine faunal constituents are known to have been introduced by human agency (Sterrer, 1986, 1998), a process that is independent of current polarity or geographic distance.

The genus *Lasaea* is composed of minute, crevice-dwelling, intertidal clams that have a near-cosmopolitan distribution on rocky shores; its North Atlantic lineages are exclusively composed of direct-developers (Ó Foighil, 1989). Molluscan systematists generally recognize one North Atlantic species, *Lasaea adamsi* (Gmelin) (= *L. rubra* Montagu; *L. bermudensis* Bush) (Sterrer, 1986). This systematic conclusion is based solely on shell characters and has not been corroborated by population genetic (Tyler-Walters and Crisp, 1989) and phylogenetic (Ó Foighil and Smith, 1995; Ó Foighil and Jozefowicz, 1999) studies. Ó Foighil and Jozefowicz (1999) constructed molecular phylogenetic trees for North Atlantic *Lasaea* lineages based on mitochondrial (mt) 16S gene variation in two continental putative source populations (Florida, the northern limit of distribution in North America; Iberia) and two oceanic island populations (Bermuda, Azores). No ampho-Atlantic genotypes were detected; Bermudan lineages co-clustered exclusively with Floridian congeners to form a western Atlantic clade and Azorean samples formed an exclusive clade with Iberian haplotypes. The western Atlantic lineages showed low levels of genetic diversity (a single Florida haplotype differed by one diagnostic nucleotide substitution from three Bermudan haplotypes), formed a shallow polytomy, and (remarkably) were sister to polyploid Australian clonal congeners in global phylogenetic trees (Ó Foighil and Jozefowicz, 1999).

Jackson (1986) attributed the presence of Caribbean species lacking an extended pelagic larval stage on Bermuda to colonization *via* rafting events from continental source populations. Based on present-day circulation patterns in the western North Atlantic, the hypothesis that Bermudan *Lasaea* populations were established by rafting events assumes that intermittent gene flow has occurred, over evolutionarily significant timeframes, from western continental margin source populations—for example, from south Florida. Island lineages are predicted to represent a subsample of mainland genetic diversity, and to contain endemic genotypes that cluster in the terminal tips of a western Atlantic clade. Ó Foighil and Jozefowicz's (1999) preliminary 16S data set had some features that were consistent with the rafting hypothesis: the three Bermudan haplotypes had close phylogenetic links to, but were genetically distinct from, the Floridian haplotype. However, these workers were unable to distinguish among ancestral and derived relationships among the four polytomous western Atlantic mt 16S genotypes, and it was unclear how representative the sole Floridian haplotype, sampled from a single population, was of mainland regional genetic diversity.

The aim of the present study was to perform a compre-

hensive cladistic analysis of Bermudan and Floridian *Lasaea* mitochondrial lineages to test their adherence to rafting hypothesis predictions. In addition to three Bermudan populations, four populations of *Lasaea* were sampled along 250 km of contiguous southeastern Floridian coastline. A total of 124 specimens of western Atlantic *Lasaea* were sequenced for a 655-nucleotide (nt) fragment of cytochrome oxidase I, a protein-encoding mitochondrial gene that, for recently diverged lineages, typically accumulates substitutions at a faster rate than does 16S (Ó Foighil *et al.*, 1998). Twelve western Atlantic haplotypes were obtained and yielded a phylogenetic tree topology that was a mirror image of that predicted by the rafting hypothesis.

Materials and Methods

Specimens of *Lasaea* were sampled in April 1998 from four southeastern Florida locations (Sebastian Inlet State Park, Brevard County; Fort Pierce Inlet State Recreation Area, St. Lucie County; Phil Foster Park, West Palm Beach; and Bill Baggs Cape Florida State Recreation Area, Key Biscayne) spanning about 250 km of contiguous coastline (see Fig. 1). The bivalves were moderately abundant in the interstices of barnacle tests at three of the sites; however, intensive sampling at the Key Biscayne site yielded only four individuals. Additional collections were taken in May 1998 from intertidal algal tufts and barnacle test interstices at three Bermudan locations (Boaz Island, the main Island at North Shore Road, and St. George's Island at the Bermuda Biological Station for Research) spanning about 20 km of the archipelago's length. At each sampling location, clams were taken from a number of microsites on the shore and pooled prior to fixation in 95% ethanol; thus a representative sample of genetic diversity from the study population was obtained.

Extensive sampling of ostensibly suitable intertidal crevice habitats elsewhere in the Caribbean by the second author (Lower Florida Keys; Dry Tortugas; New Providence, Bahamas; Puerto Rico), and by A. Frias-Martins (Jamaica), yielded no further specimens of *Lasaea*. Attempts to amplify the target gene fragment from a single dried museum specimen sampled from Belize (USNM# 841332) and from a small number of preserved specimens sampled from Cabo Tres Puntas, Venezuela (R.C. Bullock, University of Rhode Island, pers. comm.) were also unsuccessful. In the absence of tractable Caribbean outgroup samples, we generated homologous cytochrome oxidase subunit I (CO I) sequences from Sydney samples of Australian direct-developing polyploid *Lasaea* lineages (Ó Foighil and Thiriot-Quévroux, 1999) that are sister to the study populations in global phylogenetic trees (Ó Foighil and Jozefowicz, 1999; Taylor and Ó Foighil, 2000).

Twenty individuals from each of six study populations, and all four specimens from Key Biscayne, were genetically characterized by amplifying and directly sequencing a homologous

655-nt fragment of the mitochondrial CO I gene. DNA templates for thermal cycle amplification were individually extracted from entire adult *Lasaea* specimens using a QIAamp tissue kit (QIAGEN Inc.). The Folmer *et al.* (1994) CO I primer set (5'-GGTCAACAAATCATAAAGATATTGG-3'; 5'-TAAACTTCAGGGTGACCAAAAATCA-3') was used to amplify and to sequence the target gene fragment. A negative control (no template) was included in each run of 35 cycles of amplification (1 min 94°C denaturing, 30 s 45°C annealing, 1 min 72°C extension). Double-stranded products were isolated on 1% agarose gels, excised under long-wavelength UV light, and extracted using a GeneClean (Bio 101) NaI/glass powder kit. Both strands on the target fragments were cycle-sequenced using a Big Dye DNA sequencing kit (PE Applied Biosystems), and reaction products were electrophoresed on an ABI 377 automated DNA sequencer. Sequence alignments were initially performed by the CLUSTAL option of Sequence Navigator 1.0.1 (Kececioglu and Myers, 1994) and then optimized manually. Sequences were analyzed using an unweighted maximum parsimony approach (PAUP* 4.0b2a; Swofford, 1998), and root probabilities for individual haplotypes were estimated using the Castelleo and Templeton (1994) heuristic technique. Nucleotide mismatch distribution (Schneider *et al.*, 1999) and lineage-through-time (Nee *et al.*, 1996) analyses were respectively performed on the Bermudan lineages using Arlequin 2.0 (beta 2; Schneider *et al.*, 1999) and the Endemic-Epidemic Phylogenetic Process Analysis (Rambaut *et al.*, 1997).

Results

Alignment of the 655-nt CO I fragment sequences obtained from the 124 individuals of western Atlantic *Lasaea*

Table 1

Alignment of the 10 variable sites in the 655 nucleotide fragment of CO I sequenced for 12 western North Atlantic *Lasaea* COI genotypes (Genbank accession #s: AF152564, AF182733-AF182743)

	1	2	2	2	2	3	3	4	4	5
	9	4	6	8	8	0	4	0	7	3
	5	5	4	4	7	5	4	7	9	9
FL1	C	C	C	A	A	A	A	A	A	A
FL2	C	C	C	A	A	A	A	A	A	G
BDA1	C	C	C	A	A	A	A	A	G	A
BDA2	C	C	C	A	G	A	A	A	G	A
BDA3	C	C	C	G	A	A	A	A	G	A
BDA4	C	T	C	A	A	A	A	A	G	A
BDA5	C	C	C	A	A	A	G	A	G	A
BDA6	T	C	C	A	A	A	A	A	G	A
BDA7	C	C	C	A	G	A	T	A	G	A
BDA8	C	C	C	A	A	A	A	G	G	A
BDA9	C	C	C	A	A	G	A	A	G	A
BDA10	C	C	T	G	A	A	A	A	G	A

Positions of the variable sites within the sequenced fragment are presented vertically above the nucleotide columns. The prefixes FL and BDA respectively indicate haplotypes found in Floridian and Bermudan populations, and these show one diagnostic difference (in bold).

Table 2

Relative distribution of the 12 western North Atlantic *Lasaea* COI genotypes among the 7 sampling locations

	F L 1	F L 2	B D A 1	B D A 2	B D A 3	B D A 4	B D A 5	B D A 6	B D A 7	B D A 8	B D A 9	B D A 10
FL, SI	20	—	—	—	—	—	—	—	—	—	—	—
FL, FP	20	—	—	—	—	—	—	—	—	—	—	—
FL, PB	19	1	—	—	—	—	—	—	—	—	—	—
FL, KB	4	—	—	—	—	—	—	—	—	—	—	—
BDA, BS	—	—	8	—	—	7	—	2	—	1	1	1
BDA, NS	—	—	4	7	9	—	—	—	—	—	—	—
BDA, BI	—	—	5	9	—	1	2	—	2	1	—	—
Totals	63	1	17	16	9	8	2	2	2	2	1	1

The prefixes FL and BDA respectively indicate haplotypes found in Floridian and Bermudan populations. SI: Sebastian Inlet; FP: Fort Pierce; PB: Palm Beach; KB: Key Biscayne; BS: Biological Station; NS: North Shore; BI: Boaz Island. Twenty individuals were sequenced from each sampling site except for Key Biscayne, where only four specimens were obtained.

revealed 10 variable sites and 12 haplotypes (Table 1). Of the 11 nucleotide substitutions (all synonymous) detected, 8 were third codon transitions, 2 were first codon transitions, and 1 was a third codon transversion. Genetic divergence levels among the haplotypes was very low, with a maximum of four substitutions (0.6%) among pairwise comparisons. Floridian and Bermudan haplotypes exhibited one diagnostic third codon transition—*i.e.*, no haplotype was shared among these two regional groupings. Table 2 shows the

distribution pattern of the 12 haplotypes among the seven sampling sites. There was a striking discrepancy in the relative levels of haplotypic diversity and frequency in the Bermudan and Floridian samples. A total of 10 mt genotypes were contained in the combined oceanic island samples, none of which exceeded a frequency of 0.28. With the exception of a single individual from the Palm Beach population, the Floridian specimens were monomorphic for haplotype FL1.

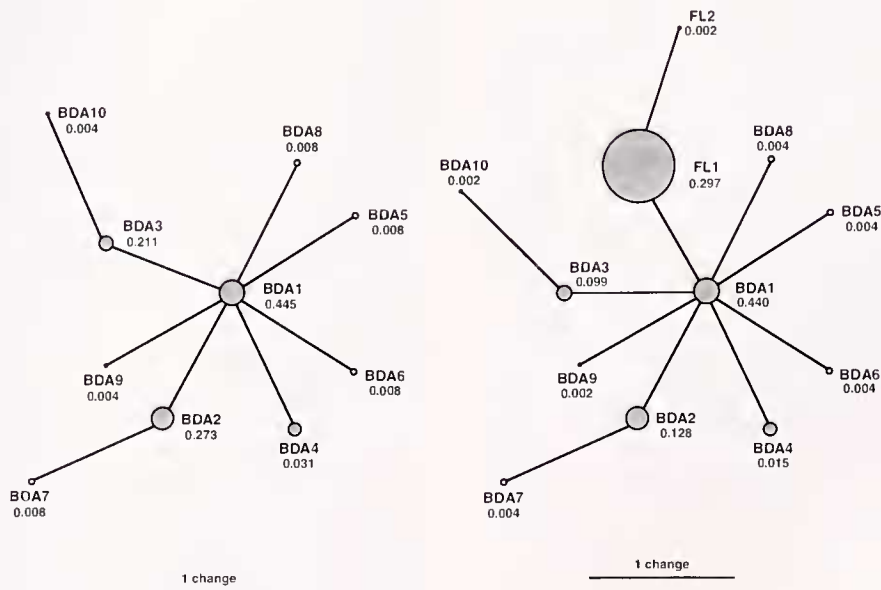


Figure 2. Unrooted phylograms of the 10 Bermudan (a) and 12 western Atlantic (b) *Lasaea* COI genotypes encountered in this study. Prefixes BDA and FL respectively identify Bermudan and Floridian lineages, and values underneath lineage titles indicate the relative outgroup weighting calculated for that haplotype. The diameter of the shaded spherical symbol associated with each haplotype is proportional to its relative frequency in the respective data sets (Table 2).

Figure 2a shows the single most parsimonious unrooted phylogram (9 steps; 2 parsimony-informative characters; CI = 1.0; RI = 1.0) obtained by exhaustive PAUP analysis of the 10 Bermudan haplotypes. This unrooted tree had a starlike topology in which there was a distinct lack of structure: 7 of the 10 haplotypes had only a single connection. A central topological position was occupied by BDA1, the most common Bermudan genotype, which was present in all three sampled sites and was one step away from 7 of the 9 other island CO I genotypes. Heuristic estimation of outgroup weighting (Castelloe and Templeton, 1994) for each of the Bermudan mt genotypes yielded a maximum value (0.445) for BDA1 (Fig. 2a), indicating that this is probably the oldest haplotype in the Bermudan dataset.

Phylogenetic analysis of the combined Floridian/Bermudan dataset (Fig. 2b) produced a single most parsimonious tree (11 steps; three parsimony-informative characters; CI = 1.0; RI = 1.0) that maintained a starlike topology and a central position for BDA1. Floridian haplotypes were peripherally positioned in a single branch of the tree topology. BDA1 was one step removed from eight western Atlantic haplotypes, including the predominant mainland lineage (FL1), and two steps away from the remaining three lineages. In contrast, FL1 was respectively, one, two and three steps removed from two, seven, and two western Atlantic lineages. Heuristic outgroup weighting of the haplotypes in the combined tree topology (Fig. 2b) identified BDA1 (0.440) as the oldest haplotype in the western North Atlantic dataset.

Caribbean outgroup populations were unavailable to root our western North Atlantic gene tree, so we generated homologous CO I sequence for an Australian direct-developing polyploid *Lasaea* lineage (GenBank# AF153064) that is sister to western Atlantic congeners in global phylogenetic trees (Ó Foighil and Jozefowicz, 1999; Taylor and Ó Foighil, 2000). The Australian haplotype differed by $\geq 4.4\%$ from the western Atlantic lineages, and its utilization as an outgroup taxon produced a single most parsimonious tree (not shown; 39 steps, CI = 0.667, RI = 0.555) in which the ingroup topology (11 steps total length) was identical to that of Figure 2b and the outgroup taxon connected to BDA7, a peripheral Bermudan haplotype (Fig. 2b), by a relatively enormous branch length of 28 steps. The basal positioning of BDA7 resulted from it sharing a thymidine at position 344 with the outgroup, whereas other western Atlantic lineages had either an adenine or guanine residue (Table 1).

Discussion

The COI data set corroborates Ó Foighil and Jozefowicz's (1999) preliminary mt 16S characterization of Floridian and Bermudan *Lasaea* populations: they are genetically very similar, yet distinct, and genetic diversity levels

are higher in the oceanic island samples. Surprisingly, the parsimony network generated was a mirror image of *a priori* source and founder topological expectations: continental populations contained a small number of endemic genotypes that positioned peripherally in the western North Atlantic *Lasaea* network (Fig. 2b). Rooting of this network is necessary to test dispersal hypotheses for these two regional populations; however, rooting is complicated by the unavailability of Caribbean outgroup genotypes.

Two rooting procedures were used: phylogenetic analyses utilizing an Australian sister lineage, and calculation of relative outgroup weights for individual haplotypes based on neutral coalescence expectations. BDA7, a relatively rare Bermudan haplotype, was identified as the root of the western North Atlantic clade when an Australian sister taxon was utilized as an outgroup. This result should be viewed with caution because of the 28:1 ratio of outgroup-to-ingroup branch lengths in the analysis and because of the peripheral positioning of BDA7 in unrooted analyses (Fig. 2b). Closely related species frequently fail to accurately root intraspecific trees if intraspecific differences are much less than interspecific differences (Templeton, 1992), and coalescence theory predicts that rare haplotypes occupying cladogram tips are likely to be recently derived lineages (Donnelly and Tavaré, 1986).

According to coalescence theory, the probability that a given haplotype is the oldest in a population is a function of its frequency and the centrality of its positioning in topological networks (Donnelly and Tavaré, 1986; Crandall and Templeton, 1993, 1996; Beckenbach, 1994). Castelloe and Templeton's (1994) heuristic method weights interior haplotypes more heavily than tip haplotypes and differentially weights interior haplotypes by their mutational connectedness and their proximity to high-multiplicity haplotypes. It unambiguously identified BDA1, the centrally positioned (Fig. 2a) and most common Bermudan haplotype (Table 2), as the most likely candidate for the oldest Bermudan mitochondrial genotype (outgroup weight = 0.445) in our sample. BDA7 is two steps away from the central topological position (Fig. 2a), received a much lower outgroup weighting (0.008), and cannot be accepted as the putative ancestral Bermudan lineage.

Haplotype BDA1 maintained its topological centrality and its high (0.44) outgroup weighting (Castelloe and Templeton, 1994) in combined analyses of Bermudan and Floridian lineages (Fig. 2b). Although the mainland haplotype, FL1, is by far the most common haplotype in the combined data set, its peripheral positioning in the phylogram and lack of connectedness to most of the other western North Atlantic haplotypes give it a relatively low outgroup weighting (0.297). Surprisingly, our analyses based on coalescence theory expectations indicate that the Bermudan lineage BDA1 is the oldest in our data set and represents the

putative ancestral haplotype for both regional western North Atlantic populations.

Phylogenetic trees represent inferred historical relationships, and our CO I dataset, when rooted with BDA1, reveals a countercurrent topology of source (Bermuda) and founder (Florida) populations. Countercurrent gene-flow patterns have also been recently inferred for a variety of marine invertebrates (Palumbi *et al.*, 1997; Palumbi, 1997; Benzie, 1999; Lessios *et al.*, 1999; Ó Foighil and Jozefowicz, 1999) and may indicate that contemporary gene flow is insufficient in these cases to obscure genetic structuring produced under previous current regimes (Benzie, 1999). However, it is difficult to envisage a plausible countercurrent dispersal mechanism for the Floridian and Bermudan study populations. Although it has fluctuated in intensity, the Florida Current has apparently been a persistent feature of the North Atlantic Gyre (Keffer *et al.*, 1988; Lynch-Stieglitz *et al.*, 1999; Duplessy, 1999). In addition, unstudied Caribbean populations are much more plausible sources of Floridian lineages, and diagnostic genetic differences among island and mainland populations for two mitochondrial genes (COI and 16S [Ó Foighil and Jozefowicz, 1999]) rule out historical (anthropogenic) countercurrent gene flow.

It may be pertinent that the low values observed for genetic diversity are consistent with an evolutionarily recent origin for *both* regional *Lasaea* populations. The most detailed fossil-calibrated estimates of molluscan gene divergence are provided by Collins *et al.* (1996) for the marine snail *Nucella* (2%/myr/lineage for [predominantly synonymous] third codon transitional differences). The central mitochondrial genotype, BDA1, is a maximum of two nucleotide substitutions removed from all of the other members of the western Atlantic *Lasaea* clade. Although complicated by phylogenetic and other potential biases, application of the Collins *et al.* (1996) rate yields a crude maximum age estimate of 0.229 Ma for the entire western Atlantic clade and also for the Bermudan population. Intrapopulation allelic relationships are modulated by demographic history (Slatkin and Hudson, 1991; Nee *et al.*, 1996; Lavery *et al.*, 1996), and it is possible that the observed patterns of CO I gene variation stem from divergent demographic processes experienced by these two evolutionarily recent regional populations, rather than from a countercurrent pattern of gene flow.

Application of coalescence theory assumes that the study populations are at equilibrium. However, this assumption may not be met by our data set. Domination of the Floridian regional population by a single haplotype (FL1) is consistent with either a recent founder event from an unstudied source population, or else with a history of population size bottlenecking; a process that promotes stochastic elimination of novel and rare haplotypes. In contrast, the starlike allelic topology of the Bermuda samples is characteristic of

a population founded by one ancestral type (presumably BDA1) that has experienced a phase of rapid growth, a process associated with lowered stochastic elimination of novel and rare lineages (Avice *et al.*, 1984; Slatkin and Hudson, 1991). Further support for this demographic interpretation of the Bermudan population was obtained when a lineages-through-time analysis (Nee *et al.*, 1996) (not shown) yielded profiles consistent with a historically growing population. However, nucleotide mismatch distribution analysis of the Bermudan population using Arlequin (Schneider *et al.*, 1999) failed to meet the sudden-expansion model (C. Cunningham, Duke University, pers. comm.), implying that the primary wave of growth for this oceanic island population may have occurred soon after the initial founding event. Differential historical rates of loss/gain of novel haplotypes in the two regional populations could act to displace ancestral haplotypes from central topological positions in the western Atlantic clade. For instance, if we were to assume that the mainland lineage FL1 represents the "true" ancestral haplotype in our western Atlantic data set, its noncentral position in the tree (Fig. 2b) might result from the repeated pruning of rare novel Floridian mt genotypes, one step removed from FL1, by sequential episodes of mainland population constrictions.

The demographic distinctions implicit in the mitochondrial genetic structure of Floridian and Bermudan *Lasaea* populations ultimately reflect environmental differences in the intertidal crevice habitat of this organism among the oceanic island and mainland locations. In Bermuda, *Lasaea* are easily sampled wherever such habitats exist (Ó Foighil, pers. observ.). In Florida, and in other Caribbean locations we investigated, *Lasaea* was respectively much more sporadic or nonexistent. This small clam seems to be a relatively rare component of the Caribbean rocky shore fauna. Indeed, apart from two lots from the Bahamas and a single individual from Belize, all museum records of western North Atlantic *Lasaea* examined in a previous survey (Ó Foighil, 1989) were from Bermuda and southern Florida.

Because of their reduced biotic diversity, oceanic islands may allow some taxa to escape competitive interactions that severely reduce survivorship in other parts of their geographic range (Paulay, 1994). Although we cannot rule out a contributing role for physical environmental factors, Bermuda may well represent such an ecological release for western Atlantic *Lasaea* lineages. If this interpretation is correct, future characterization of the genetic structure of Caribbean *Lasaea* populations, though likely to uncover novel haplotypes, is predicted to yield depauperate genetic profiles similar to that exhibited by our Floridian samples.

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Literature Cited

- Abbott, R. T., and R. H. Jensen. 1967. Molluscan faunal changes around Bermuda. *Science* 155: 687–688.
- Avise, J. C., J. E. Neigel, and J. Arnold. 1984. Demographic influences on mitochondrial DNA lineages survivorship in animal populations. *J. Mol. Evol.* 20: 99–105.
- Beckenbach, A. T. 1994. Mitochondrial haplotype frequencies in oysters: neutral alternatives to selection models. Pp. 188–198 in *Non-neutral Evolution: Theories and Molecular Data*, B. Golding, ed. Chapman and Hall, New York.
- Benzie, J. A. II. 1999. Genetic structure of coral reef organisms: ghosts of dispersal past. *Am. Zool.* 39: 131–145.
- Carlton, J. T. 1989. Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Conserv. Biol.* 3: 265–273.
- Carlton, J. T., and J. B. Geller. 1993. Ecological roulette: the global transport of non-indigenous marine organisms. *Science* 261: 78–82.
- Carlton, J. T., and J. Hodder. 1995. Biogeography and dispersal of coastal marine organisms: experimental studies on a replica of a 16th-century sailing vessel. *Mar. Biol.* 121: 721–730.
- Castelloe, J., and A. R. Templeton. 1994. Root probabilities for intraspecific gene trees under neutral coalescent theory. *Mol. Phylogenet. Evol.* 3: 102–113.
- Collins, T. M., K. Frazer, A. R. Palmer, G. J. Vermeij, and W. M. Brown. 1996. Evolutionary history of northern hemisphere *Nucella* (Gastropoda, Muricidae): molecular, morphological, ecological and paleontological evidence. *Evolution* 50: 2287–2304.
- Crandall, K. A., and A. R. Templeton. 1993. Empirical tests of some predictions from coalescent theory with applications to intraspecific phylogeny reconstruction. *Genetics* 134: 959–969.
- Crandall, K. A., and A. R. Templeton. 1996. Applications of intraspecific phylogenetics. Pp. 81–99 in *New Uses for New Phylogenies*, P. H. Harvey, A. J. Leigh Brown, J. Maynard Smith, and S. Need, eds. Oxford University Press, Oxford.
- Donnelly, P., and S. Tavaré. 1986. The ages of alleles and a coalescent. *Adv. Appl. Probab.* 18: 1–19.
- Duplessy, J.-C. 1999. Climate and the Gulf Stream. *Nature* 402: 593–595.
- Folmer, O., M. Black, W. Hoeh, R. Lutz, and R. Vrijenhoek. 1994. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.* 3: 294–299.
- Harmon, R. S., H. P. Schwarz, and D. C. Ford. 1978. Late Pleistocene sea level history of Bermuda. *Quat. Res.* 9: 205–218.
- Harmon, R. S., L. S. Land, R. M. Mitterer, P. Garrett, H. P. Schwarz, and G. J. Larson. 1981. Bermuda sea level during the last interglacial. *Nature* 289: 481–483.
- Hateley, J. G., and T. D. Sleeter. 1993. A biochemical genetic investigation of spiny lobster (*Panulirus argus*) stock replenishment in Bermuda. *Bull. Mar. Sci.* 52: 993–1006.
- Helmuth, R., R. R. Veit, and R. Holberton. 1994. Long-distance dispersal of a subantarctic brooding bivalve (*Gaunardia trapesina*) by kelp-rafting. *Mar. Biol.* 120: 421–426.
- Ingólfsson, A. 1995. Floating clumps of seaweed around Iceland: natural microcosms and a means of dispersal for shore fauna. *Mar. Biol.* 122: 13–21.
- Jackson, J. B. C. 1986. Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. *Bull. Mar. Sci.* 39: 588–606.
- Jackle, W. B. 1994. Multiple modes of asexual reproduction by tropical and subtropical sea star larvae—an unusual adaptation for genet dispersal and survival. *Biol. Bull.* 186: 62–71.
- Jokiel, P. L. 1990. Transport of reef corals into the Great Barrier Reef. *Nature* 347: 665–667.
- Kececioglu, J., and E. Myers. 1994. Sequence Navigator, 1.0.1. Perkin Elmer Applied Biosystems, Inc., Foster City, CA.
- Keller, T., D. G. Martinson, and B. H. Corliss. 1988. The position of the Gulf Stream during Quaternary glaciations. *Science* 241: 440–442.
- Lavery, S., C. Murriz, and D. R. Fielder. 1996. Genetic patterns suggest exponential population growth in a declining species. *Mol. Biol. Evol.* 13: 1106–1113.
- Lessios, H. A., B. D. Kessing, and D. R. Robertson. 1998. Massive gene flow across the world's most potent marine biogeographic barrier. *Proc. R. Soc. Lond. B.* 267: 583–588.
- Lessios, H. A., B. D. Kessing, D. R. Robertson, and G. Paulay. 1999. Phylogeography of the pantropical sea urchin *Eucidaris* in relation to land barriers and ocean currents. *Evolution* 53: 806–817.
- Lynch-Stieglitz, J., W. B. Curry, and N. Slowey. 1999. Weaker Gulf Stream in the Florida Strats during the last glacial maximum. *Nature* 402: 644–648.
- Mitton, J. B., C. J. Berg, and K. S. Orr. 1989. Population structure, larval dispersal, and gene flow in the queen conch, *Strombus gigas*, of the Caribbean. *Biol. Bull.* 177: 356–362.
- Nee, S., E. C. Holmes, A. Rambaut, and P. H. Harvey. 1996. Inferring population history from molecular phylogenies. Pp. 66–80 in *New Uses for New Phylogenies*, P. H. Harvey, A. J. Leigh Brown, J. Maynard Smith, and S. Nee, eds. Oxford University Press, Oxford.
- Nunn, P. D. 1994. *Oceanic Islands*. Blackwell, Oxford.
- Ó Foighil, D. 1989. Planktotrophic larval development is associated with a restricted geographic range in *Lasaea*, a genus of brooding, hermaphroditic bivalves. *Mar. Biol.* 103: 349–358.
- Ó Foighil, D., and C. J. Jozefowicz. 1999. Amphi-Atlantic phylogeography of direct-developing lineages of *Lasaea*, a genus of brooding bivalves. *Mar. Biol.* 135: 115–122.
- Ó Foighil, D., and M. J. Smith. 1995. Evolution of asexuality in the cosmopolitan marine clam *Lasaea*. *Evolution* 49: 140–150.
- Ó Foighil, D., and C. Thiriot-Quiévreux. 1999. Sympatric Australian *Lasaea* species (Mollusca: Bivalvia) differ in their ploidy levels, reproductive modes and developmental modes. *Zool. J. Linn. Soc.* 127: 477–494.
- Ó Foighil, D., P. M. Gaffney, A. E. Wilbur, and T. J. Hilbish. 1998. Mitochondrial cytochrome oxidase I gene sequences support an Asian origin for the Portuguese oyster, *Crassostrea angulata*. *Mar. Biol.* 131: 497–503.
- Ó Foighil, D., B. A. Marshall, T. J. Hilbish, and M. A. Pino. 1999. Trans-Pacific range extension by rafting is inferred for the flat oyster *Ostrea chilensis*. *Biol. Bull.* 196: 122–126.
- Palumbi, S. R. 1997. Molecular biogeography of the Pacific. *Coral Reefs* 16: S47–S52.
- Palumbi, S. R., G. Grabowsky, T. Duda, L. Geyer, and N. Tachino. 1997. Speciation and population genetic structure in tropical Pacific sea urchins. *Evolution* 51: 1506–1517.
- Parker, C. E. 1971. Gulf Stream rings in the Sargasso Sea. *Deep-Sea Res.* 18: 981–993.

- Paulay, G. 1994.** Biodiversity on oceanic islands—its origin and extinction. *Am. Zool.* **34**: 134–144.
- Rambaut, A., P. H. Harvey, and S. Nee. 1997.** End-Epi: an application for inferring phylogenetic and population dynamical processes from molecular sequences. *Comput. Appl. Biosci.* **13**: 303–306.
- Scheltema, R. S. 1992.** Passive dispersal of planktonic larvae and the biogeography of tropical sublittoral invertebrate species. Pp. 195–202 in *Marine Eutrophication and Population Dynamics*. Proceedings of the 25th EMBS. G. Colombo *et al.*, eds. Olsen and Olsen, Fredensborg, Denmark.
- Schneider, S., D. Roessli, and L. Excoffier. 1999.** *Arlequin ver. 2.0: a software for population genetic data analysis*. Genetics and Biometry Laboratory, University of Geneva, Switzerland.
- Slatkin, M., and R. R. Hudson. 1991.** Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. *Genetics* **129**: 555–562.
- Spitzer, W. S. 1989.** Rates of vertical mixing, gas exchange, and new production: estimates from seasonal gas cycles in the upper ocean near Bermuda. Ph.D. Thesis, Massachusetts Institute of Technology and Woods Hole Oceanographic Institution, Woods Hole Oceanographic Institution, Woods Hole, MA. WHOI-89-30, 122 pp.
- Sterrer, W. 1986.** *Marine Fauna and Flora of Bermuda*. Wiley and Sons, New York. 742 pp.
- Sterrer, W. 1998.** How many species are there in Bermuda? *Bull. Mar. Sci.* **62**: 809–840.
- Swofford, D. L. 1998.** PAUP*: Phylogenetic Analysis Using Parsimony (* and Other Methods), Version 4. Sinauer Associates, Sunderland, MA.
- Taylor, D. J., and D. Ó Foighil. 2000.** Transglobal comparisons of nuclear and mitochondrial genetic structure in a marine polyploid clam (*Lasaea*, Lasaeidae). *Heredity* **84**: 321–330.
- Templeton, A. R. 1992.** Human origins and the analysis of mitochondrial DNA sequences. *Science* **255**: 737.
- Thurman, H. V. 1997.** *Introductory Oceanography*. 8th ed. Prentice Hall, Upper Saddle River, NJ.
- Tyler-Walters, H., and D. J. Crisp. 1989.** The modes of reproduction in *Lasaea rubra* (Montagu) and *L. australis* (Lamarck) (Erycinidae: Bivalvia). Pp. 299–308 in *Proceedings of the 23rd European Marine Biological Symposium, Swansea*. J. S. Ryland and P. A. Tyler, eds. Olsen and Olsen, Fredensborg, Denmark.
- Warmke, M., and R. T. Abbott. 1961.** *Caribbean Seashells*. Livingston, Narberth, PA. 346 pp.